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Decomposition of Wood

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I. Wood as Substrate

A. Bark

A structurally and chemically complex material like wood, if newly exposed, is immediately subject to attack by numerous micro-organisms. The wood of living and dead trees is efficiently protected by the thick, highly suberized layers of the outer bark. The thin cork layers on twigs and small branches may also act as a barrier against the colonization of wood by saprobes and pathogens as long as they are intact; only a small number of micro-organisms are able to penetrate the periderm layers. The woody tissues under uninjured bark in both living and healthy newly felled trees are generally free from micro-organisms; but as soon as they are exposed by mechanical injuries or by drying and cracking of the dead bark, numerous micro-organisms rapidly invade these new areas.

On the average, bark comprises 9–15% of a trunk volume (Harkin and Rowe, 1971). The protective action of bark is dependent on its chemical and structural properties, especially on its high content of extractives such as tannins, polyphenols, glycosides as well as fats, waxes, terpenes and steroids (Table 1) which may inhibit the growth of micro-organisms. Thin bark, rich in nutrients, may itself be invaded by a number of saprobes and some pathogens. About 40 genera of fungi, predominantly Fungi Imperfecti, have been found in the bark of living aspen and poplar species (Bier, 1961, 1963, 1964) comprising a part of its biological community and determining the susceptibility of the tree to certain diseases. The same fungi are also known as inhabitants of dead wood; some of them decompose cellulose. Except for the above investigations by Bier (1961, 1963, 1964), Bier and Rowat (1963), Garner and French (1965) and Garner (1967) on the micro-organisms of the bark of *Populus tremuloides*, ecological studies of caulosphere (Garner, 1967), comprising both the bark surface and the non-living cells within the bark, have been almost completely neglected.

TABLE I. Proximate composition of ash-free wood and bark (%)

	Softwoods		Hardwoods	
	Wood	Bark	Wood	Bark
"Lignin"[a]	24–30	45–55[b]	19–25	40–50
Polysaccharides[a]	66–72	30–48	74–80	32–45
Extractives	2– 9	2–25	2– 5	5–10
Ash[a]	0·2–0·6	up to 20	0·2–0·6	up to 20

[a] Based on extractive-free material.

[b] The data on bark lignin, although based on extractive-free material, comprises in these tables of a mixture of true lignin and of suberized phlobaphene (cork).

Reproduced with permission from Harkin and Rowe (1971).

B. Wood

Woody tissues are distinguished from other plant material by their high content of lignocellulosic material and by their very low nitrogen content, both having a negative effect on the growth and degradative activity of micro-organisms. Nevertheless, a large number of organisms acting simultaneously or in succession is capable of decomposing wood under favourable external conditions in a relatively short time (Table IV).

The nitrogen content of the wood is only 0·03–0·1% of the dry weight (Cowling, 1970) and its content of carbon-rich polymers is shown in Table II; angiosperm wood is characterized by its high content of pentosans and gymnosperm wood by its high content of hexosans and lignin. In angiosperm wood xylan is the main non-glucose sugar, whereas in gymnosperm wood mannose occurs in both homo- and heteropolymers. Timell (1967) points out that the few fibrous materials in nature that lack lignin also lack hemicellulose, while all plants that contain lignin also contain hemicelluloses. Several mono-, di-, and oligosaccharides are also found in non-polymerized form in wood (Lindeberg and Selleby, 1958; Larsson and Selleby, 1960). In woody cell walls cellulose exists partly in crystalline, partly in paracrystalline form, built up as microfibrils and elementary fibrils with a definite orientation. The space between fibrils consists of hemicelluloses, lignin and varying amounts of water, depending on the moisture content (Bailey *et al.*, 1968). The three principal components of the cell wall—cellulose, hemicellulose and lignin—are degraded by different organisms to various extents.

Typical woody cell walls consist of layers of different chemical composition and structure and are thus decomposed differently by different organisms. According to the terminology proposed by Bailey and Kerr (1935), such cell walls consist of middle lamella (ML), the isotropic, intercellular substance; primary wall (P), the cambial wall or original wall formed by the meristem; and secondary wall consisting of an outer layer (S_1), central layer (S_2), and inner layer (S_3). The term "compound middle lamella" denotes the unit composed of true middle lamella and the two adjacent primary walls. According to Kerr and Bailey (1934), the inner layers denote layers towards the cell lumen, and the outer layers those towards the middle lamella. The compound middle lamella consists mainly of lignin. The three

TABLE II. The content (%) of cellulose, lignin and pentosans in wood (reproduced with permission from Henningsson, 1962)

	Resin and fats	Lignin	Pentosans	Cellulose
Pinus	1·5 ± 0·1	28·1 ± 0·2	9·4 ± 0·2	61·0 ± 0·4
Picea	0·8–0·0	27·1 ± 0·1	8·2 ± 0·1	63·6 ± 0·2
Betula	1·4 ± 0·0	19·6 ± 0·2	27·2 ± 0·3	52·4 ± 0·4

layers of secondary cell wall are distinguished by their thickness and the orientation of microfibrils within them: S_1 and S_3 are much thinner than the middle S_2 layer. The layers of secondary cell wall contain different proportions of cellulose, hemicelluloses and lignin. The significance of the different cell-wall layers in the degradation of wood will be evident in the discussion of the various types of decay.

C. Heartwood Substances and Decay Resistance

Under conditions favouring destruction of wood by micro-organisms, sapwood is usually destroyed more quickly than heartwood. There are no records of any species in which sapwood effectively resists attack. In tree species having strong natural resistance to fungi or other destructive organisms, resistance is found in the heartwood only. Heartwood resistance varies significantly from species to species. In some species heartwood has little, if any, more resistance than sapwood, but some naturally durable woods will resist the attack of micro-organisms for many years.

Chemical factors that influence microbial attack on wood, i.e. the presence of residual cell contents, the proportion of cellulose and hemicellulose in the cell walls, the extent to which they are protected by lignin and the minor non-structural constituents, have been reviewed by Scheffer and Cowling (1966).

The resistance of the heartwood in decay-resistant species results from biologically active substances in the wood, the nature and quantity of which are believed to be genetically controlled. These compounds vary widely among different tree species (Rudman and Da Costa, 1958; Rudman, 1964). Their quantity and distribution also varies widely from tree to tree of a given species as well as within an individual tree or log (Sherrard and Kurth, 1933; Englerth and Scheffer, 1954). Extractives from wood of different trees have shown a high antifungal activity (Scheffer *et al.*, 1944; Waterman, 1946; MacLean and Gardner, 1956) and various of the toxic substances have been identified. Erdtman (1939) and Rennerfelt (1944) have isolated from *Pinus sylvestris* and other conifers toxic heartwood substances including phenolic and quinonic compounds and tropolones (Rennerfelt and Nacht, 1955) which have shown a high degree of toxicity. In eucalypts, Rudman (1965) showed the fungitoxic heartwood extractives to be polyphenolic. Tannins have also been shown to be highly toxic to some wood-rotting fungi (Zabel, 1948). The inhibitory effect of volatile oleoresin compounds on *Fomes annosus* and *Ceratocystis* species was shown by Cobb *et al.* (1968). No general correlation between density or rate of growth and natural durability has been established (Rennerfelt, 1947; Suolahti, 1948; Jørgensen, 1953; Englerth and Scheffer, 1954). The tendency of outer heartwood to be more durable than inner heartwood appears to occur fairly frequently in both hardwoods and conifers (Scheffer and Duncan, 1947; MacLean and Gardner, 1956). The low extractive content and the low decay resistance of wood near the pith have been ascribed to the "immaturity" of such wood, this wood being the product of a juvenile tree (Da Costa *et al.*, 1961; Rudman, 1965). There is a tendency for this low-durability wood to cover a similar number of growth rings in fast- and slow-growing trees (Rudman, 1963). Evidence has been given that the biologically active heartwood substances may be transformed by means of ageing to relatively non-toxic substances (Anderson *et al.*, 1962*a*, *b*; Bavendamm, 1963; Arndt and Willeitner, 1969). The principal factors, probably genetically controlled ones, that cause variation in durability, are, according to Rudman (1965): (1) the resistance of the immature heartwood produced by the juvenile tree; (2) the resistance of the mature heartwood produced by the adult tree; and (3) the rate at which biologically active heartwood extractives are transformed to extractives having a different degree of activity.

II. Organisms Decomposing Wood

A. Micro-organisms

Different kinds of organisms are involved in the process that results in the decomposition of the wood. The primary infection depends on the presence of pioneer organisms and on the condition of the wood at the initial exposure. During decay the substrate changes continuously and this, together with the interaction of the organisms themselves, results in successive changes in the micro-organisms involved in the decay process. The following groups of micro-organisms colonize and decompose woody tissues: (a) Basidiomycetes; (b) Ascomycetes; (c) Fungi Imperfecti; (d) Phycomycetes; (e) Bacteria. Representatives of these groups appear at different stages of timber degradation and act differently on wood cells. Both chemical and micromorphological effects of the attack on wood are correlated with the taxonomic groups of micro-organisms and are modified by the composition and structure of the wood (Courtois, 1963*a*, *b*, 1965; Levy, 1969).

Until quite recently, the Basidiomycetes were regarded as the principal agents of wood destruction. Findlay and Savory (1954) showed that some Ascomycetes and Fungi Imperfecti were also important in the natural deterioration of wood. Species of Phycomycetes have been found inhabiting woody tissues, especially at the initial and final stages of decomposition (Merrill and French, 1965; Käärik and Rennerfelt, 1957), but hitherto no species has been found to be able to decompose lignified cell walls. The ability of bacteria to attack wood cells, including tracheid walls, has been demonstrated by Greaves and Levy (1965), Harmsen and Nissen (1965*a*, *b*) and Courtois (1966). The greatest losses of wood substance, however, are caused by the decay fungi—the Basidiomycetes of the families Polyporaceae *sensu lato*, Thelephoraceae and Agaricaceae (Table IV).

B. Insects

1. Attack

(*a*) *Standing trees and green logs.* Mechanical destruction of wood tissues is caused by insect attack (see Edwards, Chapter 16). The attack of bark beetles (Ipidae) may begin on standing trees or green logs. The living trees are weakened and killed and some mechanical destruction of the wood is

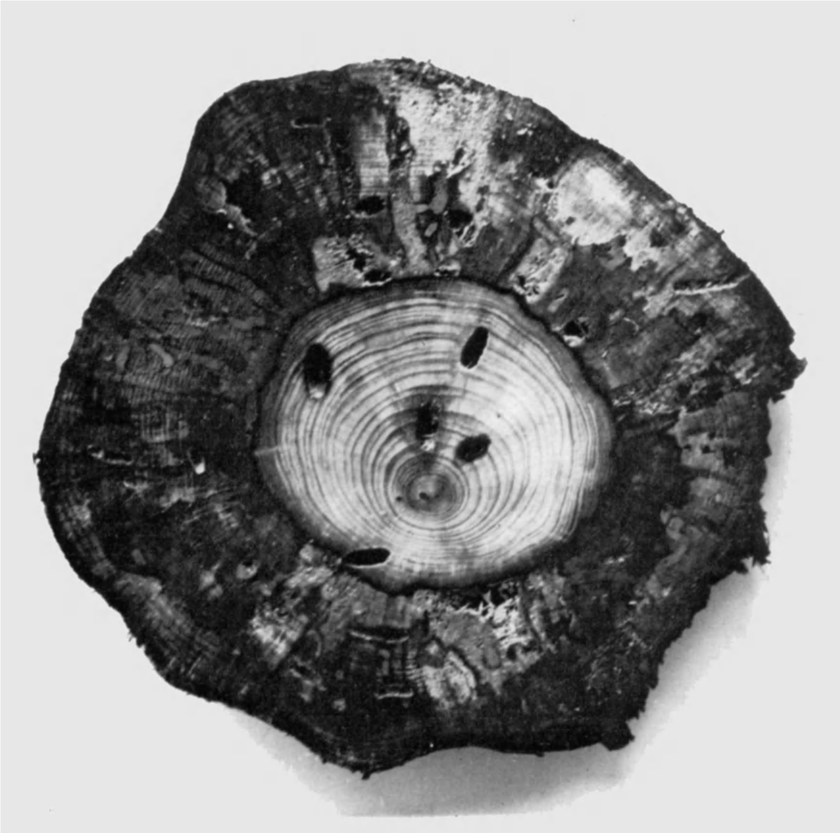

Fig. 1. Four-year-old *Pinus* stump with severe attack of sapwood by decay and blueing fungi. Sapwood and heartwood attacked by longicorn beetles. (Käärik and Rennerfelt, 1957, p. 86.)

caused by certain species, such as *Trypodendron lineatum*, whose galleries are situated deeper in the wood. This is followed by attacks of Cerambycidae (longicorn beetles) which cause considerably more destruction of heartwood (Fig. 1).

(*b*) *Seasoned wood.* Major mechanical damage is caused to seasoned wood by species of Anobiidae, Cerambycidae, Bostrychidae, Lyctidae and Curculionidae (powder-post beetles). Their larvae attack the interior of the wood, reducing it to a fine, flour-like powder or to a coarser material composed of extracted wood pellets. The tightly packed borings are held together by a thin outer shell and some intervening fibres of sound wood. Both subterranean and non-subterranean termites cause rapid mechanical decomposition of wood and other cellulosic material.

2. *Interactions with Micro-organisms*

Insects of above group (*a*) are often associated with micro-fungi, especially ambrosia fungi and blueing fungi. Many of them live in different degrees of ectosymbiosis with the fungi and distribute their specific ambrosia fungi (*Ambrosiella* spp.) or blueing fungi, mainly of the genus *Ceratocystis*, by means of more or less differentiated organs termed mycangia (Franke-Grossman, 1963). Insects of group (*b*), normally live in wood too dry for the growth of micro-organisms but nevertheless have some nutritional or physiological relationship to wood micro-organisms. The endosymbiosis of Anobiidae with bacteria and yeasts (Becker, 1942, 1943; Kelsey, 1958; Jurzitza, 1966) is well known; the decay fungi also have some influence on their development (Bletchly, 1966). Wood, attacked by fungi, attracts some termites. Results of investigations of interactions between animals and micro-organisms in wood are reviewed by Becker (1966).

III. Types of Wood Degradation

Many lignicolous fungi feed only on cell contents whilst others, after exhaustion of the ray parenchyma cells, will continue their attack by utilizing the constituents of the cell wall. A detailed survey of the different types of attack on the wood by micro-organisms from the chemical and physical points of view is given by Seifert (1968) and the micromorphological aspects are considered by Liese (1970) and Wilcox (1970).

Wood-inhabiting micro-organisms can be grouped into the following major categories according to their enzymatic activity.

(1) Fungi largely exhausting dead cell contents: not enzymatically degrading lignified cell walls:
    (*a*) moulds; (*b*) blue stain fungi

(2) Organisms capable of an enzymatic breakdown of lignified cell walls:
  (i) with a limited degradation capability
    (*c*) bacteria; (*d*) soft rot fungi
  (ii) the decay fungi, generally with a high degradation capability
    (*e*) brown rot fungi; (*f*) white rot fungi

A. Exhaustion of Cell Contents

1. *Moulds*

Mould fungi belong to the Ascomycetes and Fungi Imperfecti or in rare cases to the Phycomycetes. They mainly feed on dead cell contents and their hyphae accumulate in the ray parenchyma cells but may also be present in cell lumina of most wood elements, after penetration of pit tori (Liese and Hartmann-Fahnenbrock, 1953; Krapivina, 1962). The walls of parenchymatous cells may be completely destroyed (Scheffer and Lindgren, 1940; Lindgren, 1962). The attack of these fungi is similar to the early stages of soft rot and some fungi usually classified as moulds can also cause soft rot under suitable conditions. Merrill (1965) listed fungi that behaved as moulds in *Populus* wood but produced typical soft rot in *Quercus*. Duncan (1960) found fungi belonging to this and the following group which on certain wood species, or after an addition of nutrients, behave as soft rot fungi. An occasional attack on the surface of the cell lumen by mould fungi was reported by Merrill and French (1965).

2. *Blue Stain Fungi*

A large number of Ascomycetes and Fungi Imperfecti cause discoloration of wood due to their pigmented hyphae but otherwise this group shows wide physiological and ecological variations. These fungi are common in softwoods but are found also in hardwoods. Fungi of this group use wood as an habitat and take their nutrients from the storage material in the cells. Initially, their hyphae grow in the ray parenchyma cells, occurring only rarely in ray tracheids. In hardwoods, blue stain fungi also colonize the vessels at an early stage of infection (Campbell, 1959). The hyphae are also found in the fibres and tracheids around the rays, penetrating through the pit apertures or directly through the cell walls (Liese and Schmid, 1961). Two methods of cell-wall penetration were described by Liese and Schmid (1961): (1) For passage through the pits, the hyphae penetrate the torus without any hyphal constriction, apparently with the aid of mechanical pressure. (2) Some of the blueing fungi also penetrate tracheid walls by means of small bore-holes of about 0·2–0·6 μm, which are not widened by later growth. In *Ceratocystis pilifera* the formation of bore-holes begins with a swelling of the hyphal tip and the formation of an appressorium. From this, a fine hypha is formed which penetrates the wall by means of intercalary growth (Liese and Schmid, 1961, 1962; Schmid and Liese, 1965). As with the moulds, a number of the blueing fungi, including *Alternaria*, *Bispora*, *Chloridium* and *Phialophora* spp., have been found to cause a soft rot type of decay (Duncan, 1960).

B. Breakdown of Cell Walls

1. Bacteria

The presence of bacteria including *Bacillus*, *Pseudomonas* and *Clostridium* spp. in standing trees and in decayed wood has been known for some time (Hartley *et al.*, 1961; Basham and Taylor, 1965; Cosenza *et al.*, 1970; Shigo *et al.*, 1971) but opinions have been divided about their ability to degrade wood. Only during the last years have investigations proved their ability to decompose woody cell walls (Courtois, 1966; Greaves, 1969). Cell-wall disintegration by bacteria is a slow process but it is nevertheless a part of the continuous decomposition process of the wood, which may already begin in standing tress. Bacteria mainly attack parenchyma cells of the rays. Their cells initially accumulate on the surface of the wood and thereafter in the ray parenchyma, resin ducts and other parenchymatous cells (Boutelje and Kiessling, 1964; Greaves and Levy, 1965; Courtois, 1966). The walls of the parenchyma cells may subsequently be attacked and destroyed (Knuth, 1964; Greaves, 1965, 1968). No effect was found on the tracheids, ray tracheids and fibres (Knuth, 1964; Liese and Karnop, 1968) and vessels were only rarely attacked (Greaves, 1969). On the other hand, Harmsen and Nissen (1965*b*) and Courtois (1966) reported bacterial attack on the walls of tracheids, causing cavities and conical depressions in the wall beneath the bacterial colonies. With time, both S_3 and S_2 layers were degraded and the attack eventually continued outwards until the middle lamella was also degraded (Courtois, 1966). There is a characteristic concentration of bacteria in pit chambers and the pit membranes may be destroyed at an early stage. Different types of bacterial attack on wood are described by Courtois (1966), Boutelje and Bravery (1968) and Greaves (1969) which, however, are interpreted by Liese (1970) as different stages of development under various environmental conditions.

Bacterial attack has been found on wood after long exposure in places where the wood has a constant high moisture content (Boutelje and Kiessling, 1964; Harmsen and Nissen, 1965*b*; Liese, 1965; Boutelje and Bravery, 1968). The attack appears as random patches on the surface and in the wood, it develops very slowly and usually occurs as a mixed infection with fungi.

2. Soft Rot

A characteristic attack on the lignified cell walls by micro-fungi is called soft rot. This type of degradation is caused by fungi belonging to Ascomycetes and Fungi Imperfecti which are able to cause limited enzymatic degradation of wood. This non-Basidiomycete type of decay had been noted previously by Bailey and Vestal (1937) and Barghoorn and Linder (1944) but Savory (1954) showed the general occurrence of this type of wood decomposition and proposed the term soft rot. These fungi principally attack carbohydrates and the lignin is modified or perhaps degraded, only to a lesser extent (Seifert, 1968). This type of attack principally resembles that of brown rot in that the cellulose of the cell wall is mainly decomposed, but the micro-morphological aspect differs between these two types. It is characteristic of soft rots that the hyphae may penetrate into the cell wall and develop within the S_2 layer, causing regular and typically rhomboidal or long cylindrical cavities with conically tapered ends, formed in spiral longitudinal chains around the hyphae. The decay is restricted to the immediate neighbourhood of the hyphae. Micromorphological changes differ between hardwoods and softwoods. In both cases, attack is restricted to the ray parenchyma in its early stages and extends later to the lignified cells. In early stages, the soft rot fungi primarily penetrate through pits (Levy and Stevens, 1966). After destruction of storage materials in the cells, borehole formation begins on both radial and tangential walls (Liese, 1964) (Fig. 2).

In hardwoods, the hyphae may also attack the cell walls from the lumen, causing corrosion and subsequent lysis of the S_3 and S_2 layers (Liese, 1964). In softwoods, the S_3 layer is generally resistant to the attack of soft-rot fungi but it may be attacked in later stages of decomposition (Courtois, 1963*a*, *b*; Liese, 1965*a*, *b*). The principal location of soft-rot cavities is the S_2 layer (Courtois, 1963*a*, *b*; Corbett, 1965). Before invasion of the tracheid cell walls, the longitudinal hyphae in cell lumina branch laterally and produce fine, hyaline, perforation hyphae which grow horizontally through the S_3 layer into the S_2 layer. In the S_2 layer, often after penetrating the middle lamella, the penetration hypha branches into a T shape giving two branches parallel to the microfibrils, which grow at the same rate in opposite directions (Corbett, 1965; Levy, 1965*a*). Such T-branching was rarely found in hardwoods and in these the predominent form of decomposition consisted of V-shaped notches in the secondary cell wall (Corbett, 1965). After branching the hypha in the S_2 layer follows the spiral fibrillar structure of the layer. Formation of cavities is closely related to hyphal growth which is explained by the limited diffusion of enzymes away from hyphal surfaces (Liese, 1964; Levy, 1965*a*). The pattern of the cavities is influenced by the fungus species and the type of wood (Courtois, 1965) and also by physiological factors such as temperature and water content (Liese and Ammer, 1964; Liese, 1970). The entire secondary wall becomes perforated by confluent cavities and finally only the heavily lignified middle lamella and the S_3 layer remain, the latter then often collapsing (Liese, 1970).

The number of known species and strains of Ascomycetes and Fungi Imperfecti capable of causing soft rot in different kinds of wood is rapidly increasing. Duncan and Eslyn (1966) gave a list of about 70 species of the genera *Chaetomium*, *Sordaria*, *Xylaria*, *Peziza*, *Coniothyrium*, *Cytospora*, *Phoma*, *Pestalotia*, *Cephalosporium*, *Monosporium*, *Penicillium*, *Alternaria*, *Bispora*, *Chloridium*, *Phialophora*, *Stemphylium*, *Torula*, *Graphium*, *Stilbella*, *Stysanus* (=*Doratomyces*) and *Fusarium*. With almost every investigation of wood in contact with soil or with a high or variable moisture content, the number of known soft-rot fungi increases (Levy, 1965; Merrill and French, 1966; Butcher, 1968*a*, *b*; Gersonde and Kerner-Gang, 1968; Eaton and Jones, 1970, 1971). The attack of exclusively soft-rot fungi is found only under extreme moisture conditions. Usually, these are among the pioneers on newly exposed wood where their characteristic attack may be observed. In the later stages of wood decomposition, they are mixed

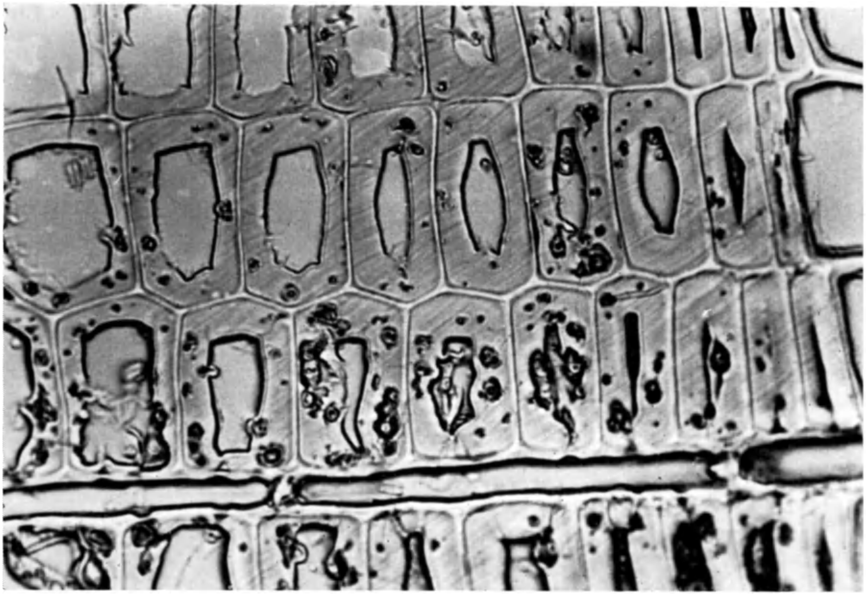

Fig. 2. Cavities in the S_2 layers of tracheid walls of *Larix europaea* Lam. et DC. caused by a soft rot fungus *Phialophora fastigiata* (Lag. et Mel.) Conant. (Courtesy of T. Nilsson.)

with other groups of fungi and their attack is difficult to distinguish. Soft-rot attack is also dependent on the wood species: a number of fungi can cause rather heavy attack on hardwood but are ineffective on softwood (Duncan, 1960; Eaton and Jones, 1971).

Thus, it is difficult to distinguish soft-rot fungi on the one hand from moulds and blue-stain fungi and on the other hand from destructive Basidiomycetes. Cavities in the secondary cell wall have sometimes been found in wood attacked by both white- and brown-rot Basidiomycetes (Duncan, 1960; Liese and Schmid, 1962; Liese, 1970). Corbett (1965) interprets the soft-rot fungi as intermediates between the blue-stain and the decay fungi. In contrast to these, the soft-rot fungi cause a rather slow deterioration on the wood surface, moving inward after the complete degradation of the outer layers (Courtois, 1963*a*, *b*); Corbett and Levy, 1963). Only rarely do they rapidly penetrate and destroy the wood (Liese, 1961; Schulz, 1964). The decomposition rates of soft-rot and decay fungi are compared in Tables III and IV.

TABLE III. Loss in dry weight of sapwood blocks attacked by Ascomycetes and Fungi Imperfecti causing soft rot. (Reproduced with permission from Bergman and Nilsson, 1971)

Fungus	Time (months)	Temperature (°C)	Weight losses %		
			Birch	Pine	Spruce
Allescheria terrestris	2	45	11·4	1·5	0·3
Aspergillus fumigatus	3	40	13·8	3·5	2·9
Ceratocystis piceae	3	RT	2·0	0	0
Chaetomium funicola	3	RT	27·6	6·0	1·3
Chaetomium globosum	3	RT	25·2	2·7	0·6
Chrysosporium pannorum	3	RT	8·3	2·6	0
Coniothryium sp.	3	RT	21·3	—	0
Cordana pauciseptata	3	RT	12·4	—	—
Gliocladium deliquescens	3	RT	7·1	1·8	—
Margarinomyces microsperma	3	RT	4·5	1·0	—
Oidiodendron tenuissimum	3	RT	17·9	2·0	—
Phialophora fastigiata	3	RT	10·0	7·3	5·6
Phialophora richardsiae	3	RT	15·8	1·7	0·5
Sporotrichum thermophile	3	45	15·4	3·1	1·2
Thermoascus aurantiacus	3	50	8·1	—	—
Trichoderma lignorum	3	RT	5·9	0·7	—
Xylogone sphaerospora	3	30	6·2	1·1	—

RT = room temperature (23–25°C.)

In summary, the following must be considered as soft-rot characteristics: (*a*) slow attack, advancing inward from the surface after destroying the outer wood layers; (*b*) destruction of cellulose and polysaccharides but not lignin; (*c*) the formation of chains of cavities in the S_2 layers of tracheids and fibres; (*d*) the greater resistance of softwoods as compared to hardwoods.

Although several explanations have been suggested for the last two phenomena, none has as yet proved entirely satisfactory (Bailey *et al.*, 1968).

TABLE IV. Losses in dry weight of *Betula* sapwood blocks attacked by different fungi. Incubation time 90 days, soil jar test method. (Reproduced with permission from Henningsson, 1965)

Group	Organism	Isolated from	Maximum weight loss %	Average weight loss %
I. More than 75% weight loss	*Fomes applanatus*	*Quercus*	78·4	72·4 ± 1·8
	Lenzites betulina	*Betula*	91·8	85·9 ± 2·6
	Polyporus hirsutus	*Quercus*	88·1	83·1 ± 1·3
	Polyporus versicolor	*Fagus*	81·7	77·9 ± 0·8
II. Weight loss 50%–75%	*Poniophorus puteana*	*Betula*	60·4	52·6 ± 2·5
	Polyporus adustus	*Betula*	65·9	56·4 ± 2·4
	Polyporus betulinus 1	*Betula*	65·1	57·4 ± 2·4
	Polyporus betulinus 2	*Betula*	58·2	52·3 ± 1·5
	Polyporus brumalis	*Betula*	61·6	50·0 ± 2·4
	Polyporus cinnabarinus	?	53·7	46·9 ± 1·5
	Polyporus frondosus	*Quercus*	74·9	63·2 ± 3·5
	Polyporus marginatus	*Pinus*	70·2	66·1 ± 0·9
	Polyporus marginatus	*Betula*	70·7	69·1 ± 0·4
	Polyporus rutilans	*Ulmus*	63·1	53·6 ± 2·2
	Polyporus sulphureus	*Quercus*	74·1	66·2 ± 2·4
	Polyporus zonatus	*Betula*	50·6	37·1 ± 3·2
	Trametes serialis	*Pinus*	61·9	55·5 ± 1·7
III. Weight loss 25%–50%	*Fomes conchatus*	?	29·0	25·7 ± 0·9
	Fomes fomentarius	*Betula*	40·5	31·8 ± 2·6
	Fomes igniarius	*Betula*	36·2	25·2 ± 3·7
	Hymenochaete rubiginosa	*Betula*	26·1	21·1 ± 0·9
	Pholiota heteroclita	*Betula*	29·9	13·8 ± 2·0
	Schizophyllum commune	*Populus*	24·6	22·4 ± 0·6
	Stereum hirsutum	*Betula*	25·4	18·1 ± 1·2

TABLE IV—*continued*

Group	Organism	Isolated from	Maximum weight loss %	Average weight loss %
IV. Weight loss 10%–25%	*Daldinia* sp.	*Betula*	24·9	22·7 ± 0·8
	Daedalea confragosa	*Betula*	16·0	12·2 ± 1·2
	Fomes connatus	*Betula*	13·4	11·5 ± 0·6
	Hymenochaete tabacina	*Populus*	15·7	9·2 ± 0·9
	Lentinus tigrinus	*Acer*	21·5	9·1 ± 3·2
	Polyporus dichrous	?	12·5	11·9 ± 0·4
	Polyporus fumosus	*Alnus*	13·3	6·6 ± 0·9
	Poria obliqua	*Betula*	13·3	10·0 ± 0·7
	Pseudeurotium zonatum	*Tilia*	11·3	7·1 ± 0·9
	Thelephora terrestris	?	11·8	7·5 ± 1·7
	Stereum purpureum	*Betula*	34·8 in 6 months	
V. Weight loss below 10%	*Coryne sarcoides*	*Picea*	7·5	5·2 ± 0·4
	Stemphylium sp.	*Betula*	9·3	7·9 ± 0·5
	Heterosporium sp.	*Betula*	6·0	4·6 ± 0·2
	No fungus		2·0	1·3 ± 0·1

Groups I–IV white and brown rot fungi; V soft rot fungi.

3. Brown Rot

This type of decay is caused by Basidiomycetes and is characterized by an enzymatic breakdown, mainly of polysaccharides of the cell wall, leaving lignin nearly unaffected. Action of brown-rot fungi on cellulose occurs in a diffuse manner through the entire cell wall. The residual lignin maintains the cell shape so that little damage to the cell wall is apparent until late stages when the residual wall collapses. In early stages the hyphae are concentrated in the rays. After the exhaustion of nutrients in the rays, they spread into the tracheids by destroying the pit tori and also by direct penetration of the cell walls (Wilcox, 1968). The perforations between the cell walls can expand during later stages of attack, leaving large openings between the cells (Pechmann *et al.*, 1967). The penetration of the cell walls is an enzymatic process and the enzymes involved are liberated both at the hyphal tips and at the lateral surfaces of the hyphae (Waterman and Hansbrough, 1957; Cowling, 1961).

A rather uniform distribution of hyphae in wood was found in hardwoods (Cowling, 1961). In *Fagus* the early colonization was concentrated in vessels rather than the rays (Greaves and Levy, 1965). The essential attack is not accomplished by bore holes but by hyphae growing on the surface of the S_3 layer in the cell lumen. The S_3 layer itself is not attacked by the brown-rot fungi (Necessany, 1963) and the removal of cell substances begins in the S_2 layer of the secondary wall (Liese and Schmid 1962*b*; Meier, 1955; Liese, 1963, 1965*b*). An advanced lysis of cell wall material in the S_2 layer found at some distance beneath the hyphae on the non-attacked S_3 layer (Liese, 1965*b*; Wilcox, 1968) indicates the ability of the enzymes to diffuse a considerable distance (Liese, 1965*b*, 1970; Wilcox, 1968). The S_1 layer and the compound middle lamella were destroyed after the decomposition of the S_2 layer (Jurasek, 1964; Wilcox, 1968). Rhomboid cavities similar to those formed by soft-rot fungi were observed in the S_2 layer (Liese and Schmid, 1962; Liese, 1963; Courtois, 1965). Another distinguishing characteristic of brown-rot attack is the irregular cell wall decomposition which occurs in patches (Schulze and Theden, 1938). The deterioration of cellulose is well advanced in groups of cells, whereas adjacent cells are only slightly attacked. The cubically cracked appearance of brown-rotted wood is explained by such irregular destruction of the cells (Fig. 3).

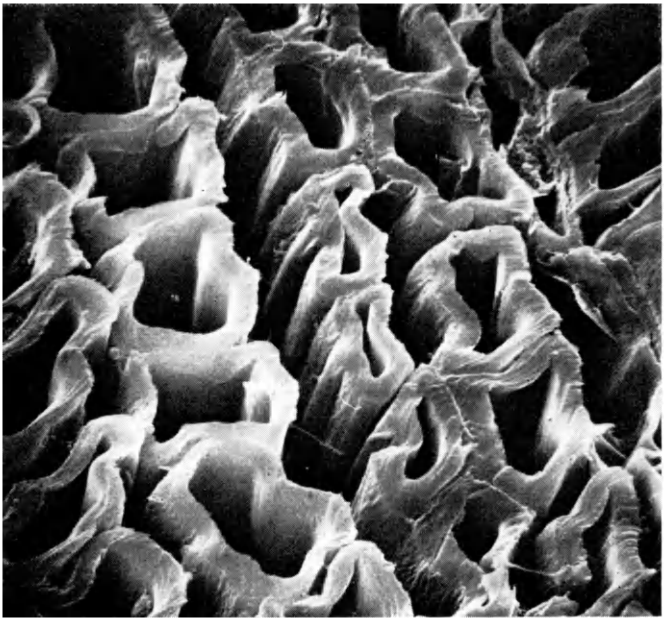

Fig. 3. Advanced stage of decay of *Pinus* sapwood by a white rot fungus, *Phellinus isabellinus* (Fr.) B. et G., middle lamella heavily attacked. Scanning micr., × 2000. (Courtesy T. Nilsson.)

In summary, it may be said that the brown rot is characterized by: (a) the decomposition of polysaccharides in the cell wall, leaving the lignin framework so that the shape is maintained until the whole cell collapses; (*b*) no thinning of the secondary cell walls until, perhaps, the very late stages of decomposition; (*c*) the action of enzymes in a diffuse manner over the entire cell wall and at a considerable distance from the hyphae; and (*d*) by the irregular patchy attack of the tissues.

A minor section of the wood decay fungi belongs to the brown rot group, as confirmed by cultural studies (Davidson *et al.*, 1938; Nobles, 1958; Käärik, 1965). Seifert (1968) noted that of 105 brown-rot fungi investigated 61 occurred mainly on coniferous wood, 29 mainly on hardwoods and 15 on both substrates. The capability of enzymatic breakdown and thus the type of decay is genetically controlled. Closely related Basidiomycetes, although specialized to different kinds of wood, produce a similar type of decay as species of *Coniophora* DC ex Fr., *Coriolellus* Murr. and *Serpula* S.F. Gray among the brown-rot fungi. Examples of degradation rates are shown in Fig. 4.

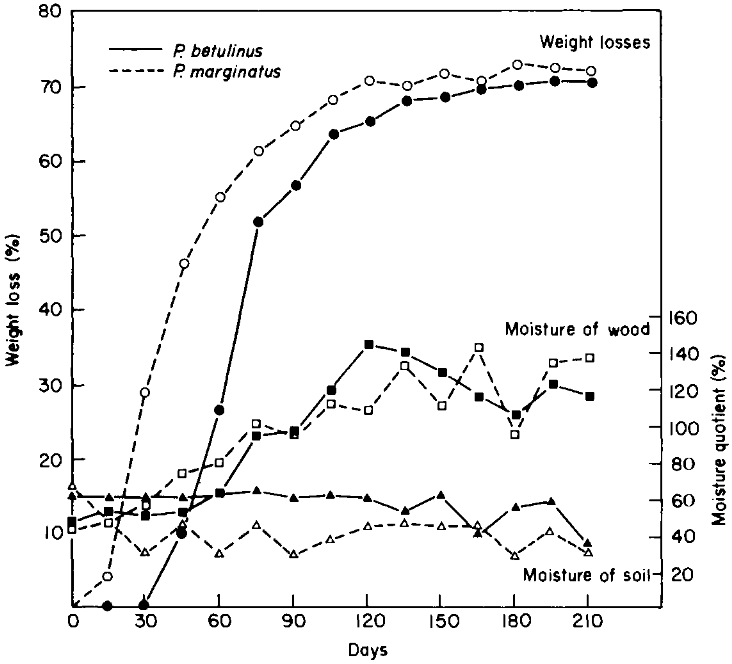

Fig. 4. Weight losses and moisture contents of wood and soil in decay tests with the brown rot fungi *Polyporus betulinus* and *Polyporus marginatus* using the soil jar method. (Reproduced with permission from Henningsson, 1965, p. 12.)

4. *White Rot*

Fungi causing white rot are characterized by enzymes capable of degrading both cellulose and lignin and they belong mainly to Basidiomycetes. Sometimes a distinction is made between white rot fungi and simultaneous rot fungi (Liese, 1970), the former decomposing wood successively, beginning with lignin and hemicelluloses and only deteriorating the cellulose at a later stage; this type of attack is often found in coniferous wood. *Fomes annosus* and *Trametes pini* cause this type of decay. Fungi causing simultaneous rot, such as *Polystictus versicolor*, preferentially attack hardwoods and simultaneously decompose all substances of the lignified cell wall. Differences between the two types have been found with the aid of fluorescence microscopy (Aufsess *et al.*, 1968) and in chemical investigations of wall degradation (Meier, 1955; Liese and Schmid, 1962; Greaves and Levy, 1965; Wilcox, 1968). On the other hand Seifert (1968), when studying chemical changes during decay processes, considered white rot and simultaneous rot to be synonyms.

In hardwoods, it has been found that the hyphae of white-rot fungi first colonize the rays and vessels extensively, entering the fibres only at later stages of decay (Cowling, 1961; Greaves and Levy, 1965). In other cases hyphae were found at early stages in all cells of both hardwoods and coniferous wood but were concentrated in vessels and rays (Wilcox, 1968). The hyphae attack lignified tissues from the ray cells, the vessels or by horizontal penetration of the cell walls. Cell wall penetration is assisted by enzymes liberated both at the hyphal tips and on the lateral surfaces, thus widening the bore holes to perforations at later stages of decay (Waterman and Hansbrough, 1957; Cartwright and Findlay, 1958; Cowling, 1961). Hyphae growing on the inside of the lignified cell lumina degrade the layers of the secondary wall from the inside, proceeding successively from the S_3 layer outwards (Cowling, 1961; Liese and Schmid, 1964; Wilcox, 1968). Lysis furrows are produced along the hyphae, deepening and coalescing with time toward the highly lignified middle lamella which is relatively resistant to attack. The cell corners are especially resistant to decomposition until very late stages of decay.

Cavities inside the secondary cell wall are found in advanced decay, resembling those of soft rot and brown rot in form and size or being of a larger size (Liese, 1970). Characteristic of the white-rot attack is the gradual thinning of the cell walls both in hardwoods and softwoods after the coalescence of the lysis zones. Variable decomposition patterns have been observed on the ray cells, pits, vessels and tracheids of different trees (Wilcox, 1970). Cell wall thinning by white rots appears very uniform from cell to cell and within each cell (Scheffer, 1936; Cowling, 1961) but with electron microscopy it was shown that minute pockets existed in both secondary wall and the compound middle lamella before the uniform thinning of the walls (Cowling, 1961). Early wood seems to be more resistant to white rot fungi than late wood (Meier, 1955; Liese, 1970) (Fig. 5).

Both chemical analyses (Cowling, 1961) and micromorphological studies (Liese and Schmid, 1964) support the view that white-rot fungi successively depolymerize cell wall substance only to such an extent that the polymerization products can be utilized consecutively for metabolism. In contrast to the brown rots whose enzymes diffuse into the inner layer of the cell wall, the enzyme action of the white-rot fungi is restricted to the cell wall layers in the immediate vicinity of the hyphae. The micromorphology of the progressive attack of the cell walls, as related to the loss of dry weight, is described by Wilcox (1968).

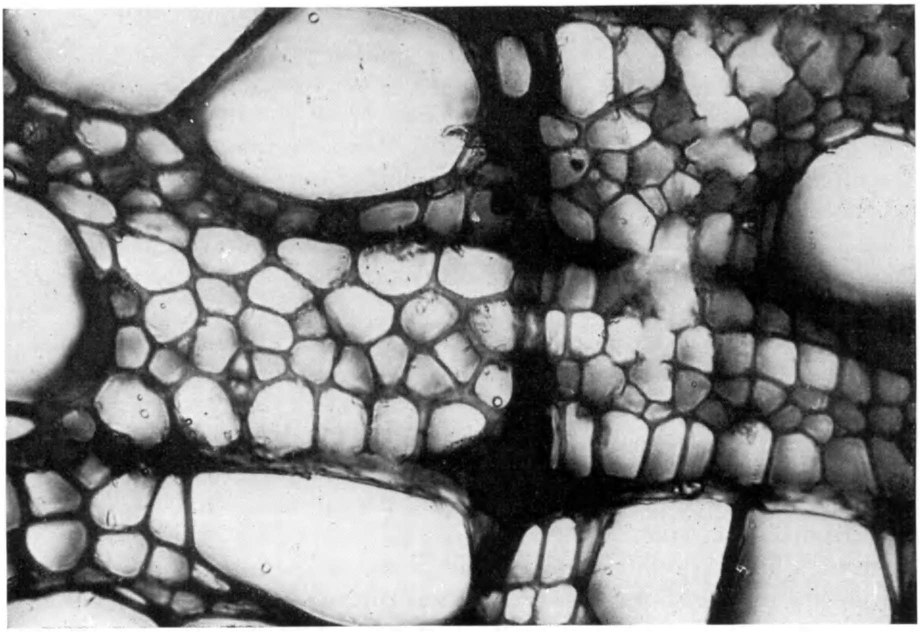

Fig. 5. Advanced decay of *Populus tremula* L. sapwood by white rot fungi. Heavy thinning of secondary cell walls. (Courtesy T. Nilsson.)

In summary it may be said of white rots that: (*a*) degradation of both lignin and polysaccharides occurs; (*b*) attack on lignified cell walls involves progressive thinning of the secondary cell walls from lumen outwards; (*c*) decomposition occurs uniformly in the regions attacked; and (*d*) the enzymes decomposing lignocellulosic material act in the immediate vicinity of the hyphae.

A large number of decay fungi belong to the white rot group and hardwood is primarily attacked: of the 250 fungi investigated in North America, 187 were on hardwoods, 45 on coniferous wood and 16 were found on both substrates (Cowling, 1961). All the many species of *Phellinus* Quél., and *Inonotus* Karst. cause white rot, whatever kind of wood they are attacking. It seems that the decay type is a phylogenetically fixed character, as pointed out by Nobles (1958). The rate of combined degradation by white- and brown-rot fungi is shown in Fig. 6.

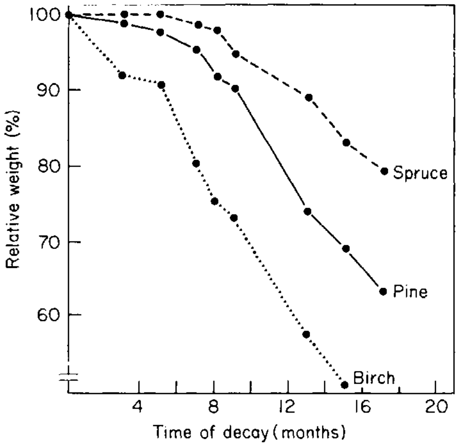

Fig. 6. Changes in relative weight during the course of decay in *Picea*, *Pinus* and *Betula* pulpwood at 20–22°C and 90–99% humidity with natural infection by common mixed white rot and brown rot fungi. (Reproduced with permission from Henningsson, 1962, p. 18.)

IV. Ecology of Wood-destroying Micro-organisms

A. Principal Factors of the Decay Process

Findlay (1966) distinguished the following main points in the development of the decay process:

(1) Establishment of infection, which depends on the following factors: (*a*) source of infection, which includes the arrival of spores or invasion by fungal mycelium from an established source; (*b*) substrate conditions, which involve the presence of a suitable substrate, a suitable temperature and an adequate supply of moisture; (*c*) the absence from the substrate of poisonous or inhibiting substances.

(2) Survival and spread of the organism in wood, where the most important factors are: (*a*) moisture content of the wood; (*b*) aeration; (*c*) temperature; and (*d*) interaction between micro-organisms.

To these factors must be added the nutrient status of the wood during the successive stages of decay.

The wood is colonized and decomposed by different associations and successions of fungi, depending on the above factors. In sections II and III decomposition of wood by representatives of different groups of micro-organisms was discussed. The resulting types of decay, as produced by one-species attack, may be found only exceptionally in naturally degraded wood, i.e. a short time after invasion by the pioneer species or under exceptional conditions when the growth of other organisms is inhibited, as in the case of soft rot of extremely moist wood. The invasion of secondary fungi largely destroys evidence of primary colonizers.

The degradation of wood is a complex process involving interactions between micro-organisms and wood and also interactions between micro-organisms themselves. Ecological investigations tracing successions from initial infection to final decomposition are few. Complementary information has been obtained from studies of forest products in use or stored in a natural environment but these studies are largely concentrated on the early stages of decay.

B. Successions of Micro-organisms

Some of the most important ecological investigations are discussed by Hudson (1968), and Shigo (1967) gives a comprehensive account of the organisms which discolour and decay wood, in which he emphasizes the complex events occurring in living trees.

D'Aeth's (1939) view of the development of fungal successions was that in the pioneer community the most aggressive organism continued to invade and alter the substrate. The substrate successively alters to an extent sufficient to permit the invasion of different organisms, which first associate and interact before the most aggressive organism again continues the invasion. This cycle continues until the substrate is decomposed.

Garrett (1963) proposed a generalized schema for fungus successions on plant remains within or upon the soil as follows:

Senescent tissue		Dead tissue	
stage 1a	stage 1	stage 2	stage 3
Weak parasites	Primary saprophytic sugar fungi, living on sugars and carbon compounds simpler than cellulose.	Cellulose decomposers and associated secondary saprophytic sugar fungi, sharing products of cellulose decomposition.	Lignin decomposers and associated fungi

This schema generally agrees with some of the successions but not with others (cf. IV E).

1. Primary Successions in Living Trees

As pointed out by Hudson (1968), it is necessary to begin the study of the decomposition of plant remains with organisms colonizing the living healthy plant and to follow the successions to final degradation. Woody plants, if healthy, show no micro-organisms in wood tissues, although bacteria and non-basidiomycete fungi, the infection courts of which have not been ascertained, have been reported from heartwood and sapwood (Lagerberg, 1935; Campbell and Davidson, 1941; Bourchier, 1961; Hartley *et al.*, 1961; Shigo, 1965*a*, *b*).

(*a*) Successions following the wounding of a living tree. There are two main types of successions colonizing wounds of living trees. After wounding a discoloration of the wood by abiotic factors appears in tissues surrounding the wound. This is followed by the invasion of the wound and woody tissues by bacteria and non-hymenomycete fungi and later with invasion by wood-decay fungi. The attack of decay fungi is in this case dependent on the primary invasion of the wood by non-decay fungi. The attack of *Phellinus* spp. follows this pattern. Another means of attack is typified by the invasion of *Stereum purpureum* and other aggressive Hymenomycete pioneers which infect only freshly exposed tissues and which, in contrast to the former group, are inhibited by non-Basidiomycete pioneer organisms. Other *Stereum* species, such as *S. sanguinolentum*, also belong to this group.

In hardwoods, the pioneer microfungi are often species of *Phialophora*, *Trichocladium*, *Coniochaeta*, *Fusarium*, *Alternaria*, *Cytospora* and *Hypoxylon*. The same species may continue their attack on dead wood on the ground.

One of the most detailed accounts of the successions of fungi colonizing living trees is that of Etheridge (1961) who studied branch infections in *Populus tremuloides*. He distinguished five stages: (1) bacteria, which were the first organisms to colonize the branches and which persisted during all the subsequent stages; (2) microfungi, with *Cystospora* spp. predominating 4 years after the death of the branches; (3) *Cytospora chrysosperma*, *Phoma*, sp., *Libertella* sp. and other fungi followed 6 years after the death of the branches; (4) the first Basidiomycetes, *Corticium polygonium* and *Polyporus adustus*, appeared after 8–9 years; (5) *Phellinus ignarius* was found on branches dead 19 years and longer. Here, too, the succession was bacteria–non-decay fungi-primary and secondary decay fungi, but compared with successions in dead wood on the ground, decay development was extremely slow.

On the whole, the same successions were found in the studies of Good and Nelson (1962) and Shigo (1963) on *Populus* trunks: in the early stages non-decay fungi were found together with bacteria and *Phellinus ignarius* var. *populinus* was only important later in the successions. Good and Nelson

(1962) described numerous non-basidiomycete fungi occurring without any clear sequence but Shigo (1963) found a few species to be more constant, viz. *Phialophora* spp., *Hypoxylon* spp. and *Trichocladium canadense.* On conifers, including *Pinus contorta* (Bourchier, 1961), *Picea glauca* (Whitney, 1962), and *Abies nordmanniana* (Shtraukh-Valeva, 1954), similar successions were found as for hardwoods above.

The successions of organisms following *Stereum sanguinolentum* infection of fresh wounds were studied by Pomerleau and Etheridge (1961) and Zycha and Knopf (1963); *Stereum* appeared to be a pioneer organism. *Fomes annosus*, *Polyporus tomentosus* and *Stereum* spp. are also pioneer invaders attacking fresh wood before other organisms (Rishbeth, 1950, 1951; Etheridge, 1961, 1963; Whitney, 1962).

(*b*) The successions of wood-decomposing fungi following attacks by parasites on living trees are not clearly established. It has been mentioned, for example, that *Nectria* canker wounds serve as invasion courts for secondary fungi (Brandt, 1964; Shigo, 1964). *Ceratocystis fagacearum* (oak wilt) is also followed by several saprophytes (Shigo, 1958).

(*c*) In fire-scars (Hepting 1935, 1941) listed the successions of Basidiomycetes during 3 years subsequent to scarring and found bacteria and Fungi Imperfecti to be associated with some Basidiomycetes.

(*d*) Fungus successions following insect attack. Living trees may be attacked by Ipidae, Scolytidae and Cerambycidae. The primary colonizers following these attacks are dependent on the tree and insect species, but yeasts, bacteria, blue stain and ambrosia fungi dominate together with other non-hymenomycetous fungi (Grosmann, 1930; Mathiesen-Käärik, 1953). The combined action of fungi and insects weaken and kill the trees, and at this stage saprophytic or weakly parasitic Basidiomycetes colonize the sapwood some 3–6 months after the initial insect attack '(Käärik, unpublished data) *Peniophora gigantea*, *Polyporus abietinus*, *P. kymatodes*. *Armillaria mellea* and *Sistotrema brinkmanni* were among the first Basidiomycetes to follow the attack of *Ceratocystis* on still living trees which had been attacked by *Ips typographus*. This type of succession is characteristic for the attack of bark beetles and closely related groups including some longicorn beetles. Other insects are known to be followed by decay fungi as follows:

On *Abies balsamea*, after an attack by Siricidae (wood-wasps), the dominant fungus was *Stereum chailletti*, accompanied by *S. sanguinolentum*, *Corticium galactinum* and *Armillaria mellea* (Stillwell, 1960). On *Pinus radiata*, *Amylostereum* sp. and *Aureobasidium pullulans*, were introduced by *Sirex noctilio*. As these declined, *Macrophoma sabinea*, *Trichoderma viride* and numerous other Fungi Imperfecti were found in the wood (Vaartaja and King, 1964).

A succession of decay fungi following an attack by *Lambdina fiscerella* (hemlock looper) was described by Engelhardt (1957). *Polyporus abietinus* was the first to attack these trees; later it was replaced by *Ganoderma* spp., *Fomes annosus*, *Armillaria mellea* and *Fomes pinicola.*

As in fungi attacking through mechanical wounds, the fungi following insect attacks on living trees are also to some extent able to continue their attack on dead wood as long as the nutritional and moisture conditions are satisfactory.

To summarize the different aspects of saprobes colonizing living trees, there are some general trends: (1) the invasion of the wood by some decay fungi is preceded by the attack of bacteria and non-decay fungi which continue to colonize the wood layers which were produced before wounding. The decay fungi are secondary colonizers of such previously occupied tissues. This succession seems to be common both in hardwoods and conifers for a number of decay fungi which attack heartwood and sapwood. (2) Some decay fungi are reported to be pioneer colonizers of wounded tissues and they generally decline after attack by other organisms. Among such fungi are listed *Fomes annosus*, *Polyporus tomentosus* and *Stereum* spp. although under other circumstances at least *Fomes annosus* and *Stereum* spp. may effectively attack dead wood and compete with other decay and non-decay fungi (Käärik, 1971).

The number of dominant non-decay fungi was found by Shigo (1963) and Etheridge (1961) to be limited; others have found rather numerous species (Good and Nelson, 1962) but their number is never as large as on newly exposed, dead wood (Merrill and French 1966; Butcher 1968*a*, *b*; Käärik, 1967, 1968). Some of the decay and non-decay fungi continue their attack after the death of the tree. Among the saprobes on living trees (Good and Nelson, 1962; Shigo, 1965), are included a number of soft-rot fungi. Little is known about their activity in living trees, but some of them have shown inhibitory action *in vitro* against wood-destroying fungi (Etheridge, 1957; Henningsson, 1967*b*).

2. Primary Successions on Dead Wood

(*a*) *Organisms attacking fire-killed trees.* The fungal successions involved in the decomposition of fire-killed trees were described for several pines, *Pinus strobus*, *P. resinosa* and *P. banksiana,* in Canada by Basham (1957, 1958). Blueing fungi belonging to Fungi Imperfecti were the first to attack the sapwood, often preceded by an attack of bark beetles. They were common for 1–3 years after the death of the tree. Already in the first year decay fungi attacked the sapwood, *Peniophora gigantea* and *Polyporus abietinus* causing 80% of the decay. After 2 years, *Polyporus anceps*, *Fomes pinicola* and *F. subroseus* dominated and heartrot caused by *Trametes pini* appeared still later. This type of colonization closely resembles the colonization of living trees attacked by insects.

(*b*) *Organisms on wind-felled trees*. Deterioration of wind-felled trees has also been investigated in North America. On conifers Buchanan (1940) found active decay fungi, mainly sapwood-attacking species, after 2 years. They were followed by *Fomes pinicola* and *F. applanatus* which were responsible for most of the decay. Stillwell (1959) found in *Abies balsamea* numerous unidentified non-decay fungi. *Stereum chailletii* and *S. sanguinolentum* were among the pioneer invaders but in advanced decay *Lenzites sepiaria* and *Polyporus abietinus* were the most important fungi. Stillwell stressed the marked similarities in fungal successions occurring in insect-attacked and wind-thrown trees. Engelhardt *et al.* (1961) found that *Stereum sanguinolentum*, the pioneer fungus of wind-thrown *Picea*, was followed by *Fomes pinicola* which was responsible for the principal decay.

Common to the wind-thrown, fire-killed and insect-killed trees, as well as to branches dying in the crowns of living trees, is the fact that relatively few species are involved in decomposition and that the process is slow or very slow as compared with the attack on wood in contact with the soil.

(*c*) *Successions on felled trees, timber, logs and posts in contact with the soil*. The most detailed ecological study of the degradation of deciduous wood is that of Mangenot (1952). *Fraxinus*, *Betula* and *Salix* were studied during a period of 3–4 years and *Fagus* and *Alnus* for shorter periods. Much of his research concerned newly cut trees but most of them had been previously colonized by active decay fungi belonging to the group which is preceded in wood by non-basidiomycetes (cf. section IV B, 1(a)). Mangenot concentrated on the invasion of dead wood by non-basidiomycete pioneer colonizers. Seven stages of decomposition were distinguished, as follows:

(1) *Phellinus* stage, with Basidiomycetes and Ascomycetes which attacked living trees and which continued as active decay fungi under a variable period of time after the death of the tree.

(2) *Phialophora fastigiata* stage, which is characterized by the invasion of the surface of the dead wood by fungi which did not penetrate deeply into the wood and which persisted until the later stages. *Phialophora fastigiata*, *Coryne sarcoides*, *Margarinomyces heteromorpha*, *Beauveria virella*, *Cladosporium herbarum* and others were found at this stage. These were considered to be a group of "sugar fungi" but it is now known that several of them are capable of causing a soft rot.

(3) *Melanomma* stage, which consisted of various Ascomycetes and Fungi Imperfecti regarded as moderate decomposers of wood which sporulate on the wood surface. *Hypoxylon*, *Ceratocystis*, *Melanconium*, *Stemphylium* and *Alternaria* were listed here.

(4) *Mortierella ramanniana* stage which is characterized as the first stage of decomposition of the wood itself. It includes both cellulolytic and sugar fungi, the last group utilizing decomposition products or remains of other fungi. *Mortierella ramanniana*, *M. pusilla* var. *isabellina*, *Chaetomium*, *Fusarium* and *Cylindrocarpon* were found here.

(5) *Leptoporus* stage involving a second invasion of decay fungi including species of *Leptoporus*, *Corticium*, *Crepidotus* and *Calocera*.

(6) *Mollisia* stage; advanced stage of decomposition. Trunks are colonized by Ascomycetes, such as *Mollisia*, *Chlorosplenium* and *Dasyscypha*, and some Basidiomycetes, such as *Exidia*.

(7) The (final) *Bisporomyces* stage included species which grow very slowly and utilize the decomposition products of the wood and the remains of other fungi. *Corticium* spp., *Caldesiella*, *Sirobasidium*, *Arachnopeziza* and *Phialophora verrucosa* were listed here.

Hudson (1968) analysed these stages and found them comparable with Garrett's general schema. The existence of the pre-death *Phellinus* stage complicates the question of the pioneer colonizers. It is quite possible that at least some of the *Phialophora* stage fungi had already colonized the wood before the *Phellinus* stage.

The succession of higher fungi on *Fagus crenata* logs in Japan was studied by Ueyama (1966) who found the following sequences: (1) wood-staining fungi such as *Ceratocystis moniliforme* already present after 10 days; (2) soil fungi, such as *Aspergillus*, *Penicillium* and *Trichoderma* from 10 days to 2 months; (3) decay fungi including *Schizophyllum commune*, *Stereum purpureum*, *Trametes sanguinea* after 1–2 months; (4) *Coriolus versicolor*, *Trametes hirsutus*, *Gloeophyllum betulinum* after 5–6 months; (5) soft cup fungi and Agaricaceae, such as *Hypoxylon coccineum*, *H. annulatum*, *Pleurotus ostreatus*, *P. japonicus* from 1 year. The primary invaders had the fastest growth rates and tolerated higher moisture contents (80%) in the wood than the following slow-growing decay fungi (65–70%). The soft cup fungi were unable to colonize freshly felled logs.

Jahn (1968*a*) observed the sporophores of macrofungi attacking living and standing dead trees, fallen trunks, slash and stumps of *Abies alba*. A heterogeneous heart-rot stage on living trees was found with *Phellinus hartigii*, *Fomes annosus* and *Bondarzewia montana* which correspond to Mangenot's *Phellinus* stage. On fallen trees colonization began on twigs with *Aleurodiscus calycinus* and *Trichoscyphella calycina*. The optimal decay phase had a wide time range of between 10–30 years and was especially characterized by *Fomes pinicola*, *Ganoderma applanatau*, *Phellinus pouzarii*, *Stereum murraii* and *S*, *chailletii* together with *Phellinus hartigii* and *Fomes annosus*. In the final phase in the soft, decayed wood, the fungi of the optimal phase disappeared and were replaced by various Agaricaceae. In dead, standing trees the wood was rapidly seasoned after shedding of the bark and decomposition which had commenced came to a standstill until the trees finally, sometimes after 40 years, fell down and were decomposed. The stumps were colonized by the same fungi as trunks on the ground. Jahn tried to distinguish different associations of regularly coexisting species in various sequences.

On felled *Fagus* trunks Jahn (1968*b*) described two different pioneer associations of fungi, one with *Bispora antennata* and *Calycella monilifera* attacking decorticated wood and the other with *Diatrype disciformis* and *Nectria cinnabarina* attacking the bark.

Primary attack and deterioration by both microfungi and decay fungi on *Betula* pulpwood in Norway was studied by Venn (1972); 25 species of microfungi and 7 species of decay fungi were isolated during an initial stage of decomposition of between 8 and 18 months. *Coriolus zonatus*, *Lenzites betulina*, *Stereum hirsutum*, *S. rugosum* and *Libertella betulina* produced high dry-weight losses. According to an analysis of variance, the interaction between species and the initial moisture content of the wood was strongly significant.

Deterioration of wooden posts in contact with soil was studied by Corbett and Levy (1963), Merrill and French (1966), Käärik (1967, 1968, 1971), Butcher (1968*a*, *b*), Kerner-Gang (1970) and Banerjee and Levy (1971). Corbett and Levy (1963) suggested the following pattern of colonization in their ecological studies on fungi associated with the decay of *Betula* and *Pinus* fence posts: (1) Moniliales group I (*Trichoderma viride*, *Penicillium* spp., *Botrytis* sp.); (2) Sphaeropsidales (including several soft-rot fungi); (3) Moniliales group II (*Gliocladiopsis*, *Cylindrocarpon* spp.); and (4) Basidiomycetes. In the survey by Merrill and French (1966) of the first 6 months' attack essentially the same pattern was obtained. Butcher (1968*a*, *b*) reported that in the above-ground zones the succession did not advance further than the mould stages. At the ground line moulds were followed by soft-rot fungi which were succeeded by an invasion of secondary moulds and Basidiomycetes. In long-term trials Käärik (1971) showed the development of the different groups of fungi over a period of 4 years. Attack by Basidiomycetes steadily increased with time although the number of species involved decreased; but fungi of the other main groups, with the exception of Phycomycetes, also remained until the late stages of decomposition. During the first years it was not generally possible to distinguish between primary and secondary moulds. The less active Basidiomycetes appeared earlier in the succession and the more active later, as was also found in deciduous pulpwood by Henningsson (1967*c*). As in all the successions described above, the active decay fungi occupied wood already extensively colonized by the different groups of non-decay fungi and they appeared to

TABLE V. The dominant Basidiomycetes on poles from different sites

Fungi	Number of isolations	Appearance in succession			Sample plots, soils					
					Moist		Normal		Dry	
		Early	Middle	Late	A	D[a]	B	E	C	F
I. Occurring on sub-soil parts										
Fomes annosus	1054	+	+++	+++			B	E	C	F
Polyporus borealis	276	+	++	+++	A		B	E	C	F
Merulius himantioides	220	+	+++	++						F
Poria vaillantii	122	—	+++	++		D	B			
Poria rixosa	120	++	++	++			B	E	C	
Poria cinerascens	91	++	+++	+		D	B		C	F
Odontia bicolor	82	+	++	—			B	E		
Merulius pinastri	37	—	++	++	A	D				F
Poria mollusca		+					B			
Polyporus fragilis				+			B			
Polyporus stipticus				+					C	
Merulius molluscus				+					C	
Mycena sp. I				+	A					
Polyporus kymatodes		+		+		D				F
II. Occurring on aerial parts										
Peniophora gigantea	848	+	+++	+++	A	D		E	C	F
Stereum sanguinolentum	360	+++	+++	+++	A	D	B	E	C	F
Polyporus amorphus	144	+++	+++	+	A	D	B	E	C	F
Peniophora pithya	124	++	+++	+		D	B		C	F
Stereum abietinum	121	+	++	+++			B			
Polyporus tephroleucus	64	—	+	++	A		B			
Fomes pinicola	53	+	++	+	A		B	E	C	
Fomes nigrolimitatus	51	+++	++	++	A		B		C	
Pleurotus mitis	20	++	—	+			B		C	F
Polyporus abietinus	10	+	++	—		D	B	E		F
Poria taxicola				+			B		C	
Stereum chailletii				+			B			
Merulius corium				+			B			
Trametes isabellina				+				E		
Merulius serpens				+				E		
Flammula penetrans				+				E		F

[a] A and D: fungi found on sample Plots A and D on moist soil; B and E: fungi found on sample plots B and E on normal soil; C and F: fungi found on sample plots C and F on dry soil.

be highly competitive with other wood-inhabiting fungi, including *Trichoderma*, *Gliocladium* and *Penicillium* (Table V).

Banerjee and Levy (1971) described the course of decomposition of wooden posts in soil as follows. At the ground line a relatively large number of bacteria and rapidly-growing fungi, mainly moulds, colonized the wood surface. After a time, fungi capable of penetration into the ray parenchyma of the sapwood, such as the blue-stain and soft-rot fungi, were isolated below the surface and fungi capable of degrading cell walls, the soft-rot fungi, were later isolated from greater depths. The Basidiomycetes appeared after some months. The initial colonization was largely a competition for nutrients. The subsequent attack of micro-organisms penetrating or degrading cell walls had the effect of altering the permeability of the wood, which resulted in better aeration as well as increasing the moisture content of the wood. According to the authors, this could possibly produce suitable conditions for the wood-rotting Basidiomycetes to penetrate deeply into the wood and utilize cell wall material as a source of nutrient.

Although decomposition of wooden posts in contact with soil has been thoroughly investigated during recent years the results and conclusions are not quite convergent because of the different investigation methods, materials and microclimatic conditions. Butcher (1971) developed an examination procedure which may lead to a subsequent statistical analysis of the results, which would be an essential step in understanding natural decay processes.

(*d*) *Decomposition of branches and slash.* Spaulding (1929) described a succession of Basidiomycetes on *Pinus strobus* slash over a period of 2–14 years. *Stereum sanguinolentum* and *Peniophora gigantea* were two pioneer fungi which acted for only a short time. *Lenzites sepiaria* and *Polyporus abietinus* also invaded the wood from the beginning but they continued the attack for 8 years. *Polyporus fragilis* and *Poria cinerascens* were found almost from the beginning until the final stages of decay. Among the late colonizers were *Corticium cinerascens*, *Merulius aureus* and *Corticium sulphureum.* In slash, extreme temperature and moisture relations are often found (Spaulding, 1929; Loman, 1965).

Spaulding and Hansborough (1944) studied fungi on slash of different hardwoods and conifers: (1) when twigs began to fall—after 2–4 years in hardwoods and 5–8 years in conifers—and (2) when small branches began to break—after 3–4 years in hardwoods and 6–10 years in conifers. In the first stage, non-hymenomycetous fungi, together with *Stereum rameale*, were most often found in hardwoods; in the next stage a large number of common Polyporaceae and a number of Ascomycetes, such as *Diatrype*, *Dermatella*, *Eutypella* and *Dasyscypha*, occurred on trunks and logs. *Libertella* and *Scoleconectria* were present from the first to the final stages.

Chesters (1950) studied the successions of fungi on dead logs and branches of deciduous trees. He found the associations of fungi to be dependent on a number of factors, of which the most important were the host species, the exact stage of decay and the microhabitat. According to Chesters, the primary colonizers are wound parasites and as such are responsible for the shedding of the branches or aggressive saprophytes which may attack moribund branches. In this group host-specific species are often found, such as *Diatrype* and *Hypoxylon* (see Pugh, Chapter 10). Among the primary colonizers are Basidiomycetes, such as *Stereum hirsutum* and *Polyporus versicolor*, on the outer layers of wood and *Ganoderma applanatum*, *Polyporus squamosus* and *P. betulinus* on heartwood, which attack through the wounds. Hudson (1968) compared this stage with Garrett's stage 1 (a) and with the *Phellinus* stage of Mangenot, and again stressed the heterogeneity of this stage.

According to Chesters secondary successions could depend on a variety of factors, of which the fractions of the wood remaining, the primary invaders and the moisture content of the wood were among the most important. A colonizer of moist wood is *Xylaria hypoxylon*, whereas on dry wood *Melanomma pulvis pyrius* and *Bertia moriformis* were found. Chesters also recognized a late stage, comparable with *Bisporomyces* stage of Mangenot with *Lasiosphaeria* and *Chaetosphaeria* amongst other species.

(*e*) *Degradation of stumps.* Rishbeth (1950, 1951) discussed the succession of decay fungi on *Pinus* stumps and showed that the fresh stumps were rapidly invaded by different fungi. *Fomes annosus* and *Stereum sanguinolentum* were only successful on substrates free from other organisms. In early stages *F. annosus* could compete efficiently with many fungi, such as *Cylindrocarpon radicicola*, but not with *Peniophora gigantea*. Later, *F. annosus* was often replaced by *Trichoderma viride* and *Torula ligniperda*. *Hypholoma fasciculare*, *Melanospora* and other blue-stain fungi followed later. Yde-Andersen (1958), Moreau and Schaeffer (1959) and Braun (1960) discussed the importance of bacteria on decay and on other organisms in stumps.

Cobb and Barber (1968) found that the susceptibility to Basidiomycetes, such as *Fomes annosus*, lasted in freshly cut stumps for at least 4 weeks, but was already declining after 2 weeks. The rate of vertical penetration depended on the season, varying from 8 to 16 cm per month for *F. annosus*. Pronounced staining of the sapwood, especially by *Ceratocystis* spp., strongly inhibited the growth of *F. annosus* in the wood.

Meredith (1959, 1960) investigated successions on *Pinus* stumps and found that the fresh surfaces acted as highly selective substrates and were colonized by a relatively small number of fungi which were able to overcome the resistance of the wound surface. The primary invaders were Basidiomycetes such as *F. annosus*, *Peniophora gigantea*, *Stereum sanguinolentum* and non-cellulolytic blue-stain fungi. The first stage was called the *Peniophora* stage and was comparable with the *Phellinus* stage of Mangenot. These fungi were dominant for 2–3 years after felling and were followed by *Hypholoma* stage with several Agaricaceae with *Hypholoma fasciculare* dominating. Some new polypores, such as *P. adustus* and *P. abietinus*, then appeared. The final, *Tricholoma*, stage was characterized by several Agaricaceae, with *Tricholoma rutilans* predominating. The number of Phycomycetes and Fungi Imperfecti present increased with the age of the stumps. Meredith also discussed the effect of the moisture content of wood on fungi. From a value of 39% of the dry weight at the surface, the moisture content increased to 88% near the ground and 131%below the ground. The mean moisture content increased with the age of the stumps, from 70% in 1-year stumps to 394% in 5-year stumps, and this could have a selective influence on the attack of fungi.

Käärik and Rennerfelt (1957) showed principally the same result for *Pinus* and *Picea* stumps in Sweden. The primary colonizers were mainly Basidiomycetes including Polyporaceae, Thelephoraceae and *Armillaria mellea*. Other Agaricaceae appeared later in succession. Numerous Fungi Imperfecti were found. Their number increased with the age of stumps. Various Mucoraceae were present especially on stumps after 4 years. The decomposition rates are shown in Figs 7 and 8.

Ginns and Driver (1970) investigated the seasonal variation of the natural stump mycobiota on freshly cut stump surfaces and found variations in the attack of different fungi. *Fomes annosus* colonized the stumps in October–December; *Trichoderma* colonization increased from the beginning of February and *Peniophora gigantea* colonized large areas during December–February. The mycobiota on each stump was found to be determined by the species of micro-organisms infecting them, by the number of their diaspores and their competitive ability. Local environmental factors affecting spore production and discharge determined to a great extent the rate of infection by airborne spores of each species.

Jahn (1962) investigated the successions of macrofungi on *Picea* stumps in the mountain area of Westfalen by sporophore observation. Variable activity was found in microclimatically different places. He distinguished three phases: (1) the initial phase on firm wood with the characteristic species being *Stereum sanguinolentum* and *Trametes abietina*; (2) the optimal phase with advanced decay in outer or inner wood layers, but with wood partially firm, depending on the microclimatic conditions, in stumps 3–8–12 years of age with characteristic species including *Naematoloma capnoides*, *N. radicosum*, *Paxillus atrotomentosus* and *Tricholoma rutilans*. This stage agrees with Meredith's *Hypholoma* and *Tricholoma* stages. (3) In the final phase the wood is completely softened. Characteristic species are *Pseudohydnum gelatinosum* and *Physisporinus sanguinolentus*, but several species from the optimal phase were still present, viz. *Osmoporus odoratus*, *Trametes serialis*, *Calocera viscosa* and *Mycena* spp. Of the 51 species noted, 90%

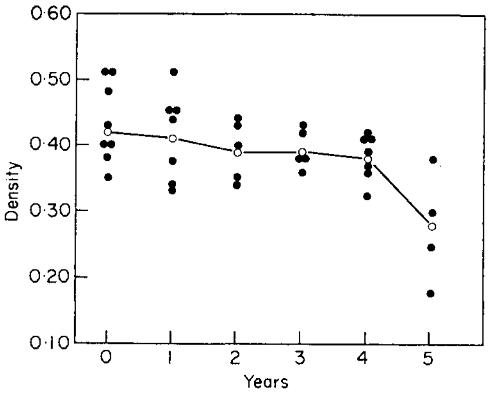

Fig. 7. Densities of stump wood samples: *Picea* sapwood in 0–5-year-old stumps showing rapidly decreasing density after 4 years. (Käärik and Rennerfelt, 1957, p. 57.)

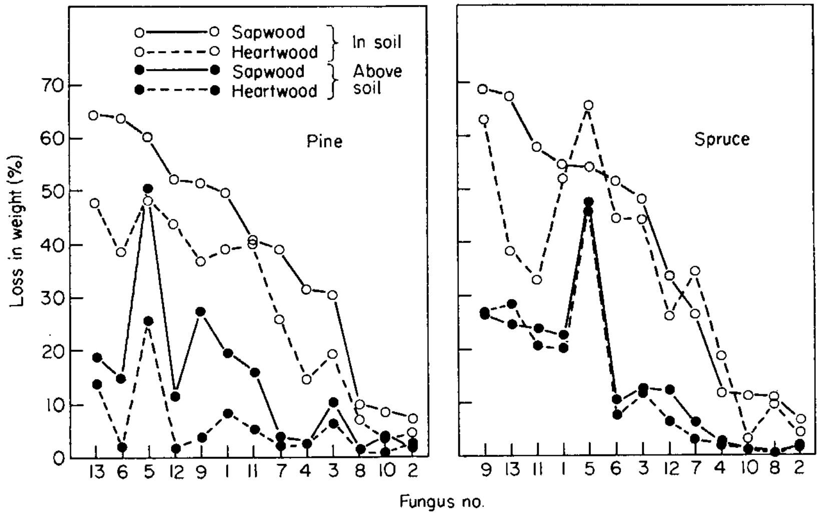

Fig. 8. Per cent weight losses caused by stump fungi on wood of *Pinus sylvestris* and *Picea* decayed 4 months above and in the soil. Fungi arranged in order of decreasing attack on sapwood in soil. Fungi: (1) *Peniophora gigantea*; (2) *Sistotrema brinkmanni*; (3) *Stereum sanguinolentum*; (4) *Polyporus abietinus*; (5) *Fomes pinicola*; (6) *Polyporus borealis*; (7) *P. stipticus*; (8) *Corticium alutaceum*; (9) *Lenzites sepiaria*; (10) *Armillaria mellea*; (11) *Fomes annosus*; (12) sterile 47–I; (13) sterile 256–X. (Käärik and Rennerfelt, 1957, p. 49.)

were found in similar localities in Central Sweden and 65% in the subalpine Piceeta in Switzerland. Some differences were noted between the dominant species on stumps and fallen trunks.

The general trend in the decomposition of stumps is that Basidiomycetes are highly active during the pioneer stage. Fungi Imperfecti and a few Ascomycetes, mainly non-cellulolytic but also of soft-rot type, are present and their number increases with the age of the stumps. Mucoraceae appear in the final stages of decay. Meredith (1960) explained the successions by the suggestion that at later stages of the decomposition the rate at which simple carbon compounds were liberated exceeded the rate of utilization by decay fungi; the accumulation of the simple carbon compounds accelerated the development of non-cellulolytic fungi.

C. Factors Influencing Microbial Attack

1. Temperature

The organisms involved in the decomposition of wood are largely mesophilic and generally unable to grow above 40°C. Some lignicolous fungi have a special tolerance to extreme temperatures. Thermophiles with an optimum temperature of between 40 and 50°C, and usually unable to grow below 20°C, have been found in piled wood chips (Bergman and Nilsson, 1971). The optimum temperature for the growth of most decay fungi is between 25 and 30°C. The blue-stain fungi show a wide temperature range for growth, with an upper limit between 32 and 40°C, and an optimal between 20 and 28°C. For many species the minimum temperature for growth lies below the freezing point. These fungi are able to propagate and spread especially inside a log at winter temperatures. For many species, short exposure to cold may even cause an increase of growth capacity when temperatures rise again (Pechmann, 1966).

The influence of high temperatures on fungi decaying *Pinus contorta* (lodgepole pine) slash was investigated by Loman (1962, 1965) in Alberta. The activity of decay fungi in logging residues is frequently limited by rapid and great fluctuations of temperature which are usually concomitant with suboptimal moisture conditions. Two fungi, *Peniophora phlebioides* and *Lenzites sepiaria*, which have high temperature optima and wide temperature tolerances, were the dominant decay fungi in the upper 5 cm of exposed slash. *Stereum sanguinolentum* and *Coniophora puteana* have lower temperature optima and narrower temperature tolerances and were mainly active at greater depths in slash pieces. The high temperature, but not the low temperature, fungi survived at temperatures between 45 and 52°C for 220 min. Lethally high temperatures for *Coniophora* and *Stereum* were measured in the upper and central parts of slash during periods of fine weather, but these temperatures were not likely to be lethal for *P. phlebioides* and *L. sepiaria*. The occasional occurrence of low-temperature fungi in the upper parts of pieces of slash suggested that they were able to invade these areas periodically during cool and rainy periods.

2. *Moisture Content of the Wood*

The limits and optima of temperature and moisture contents are stable characteristics of microbial species or sub-specific groups. They are found to vary within each group from an average which is characteristic of the group only to a limited and statistically definable extent (Ayerst, 1968). Mangenot (1952) pointed out that the superficial moisture content of the wood was one of the factors that determined the sequences of the stages of attack. Courtois (1968) employed mathematical and statistical methods to analyse the interrelationship of wood deterioration of *Pseudotsuga taxifolia* (Douglas fir) by *Fomes annosus* and the specific gravity and moisture content of the wood. Light-weight wood absorbs more water than denser wood. Therefore, as a consequence of the water reservoir wood of lower weight is more susceptible to the penetration, growth and decay activity of the fungal mycelium. Since the evaporation from wood of a lower specific gravity progresses more rapidly than that from heavier wood, deterioration which is influenced by the moisture content is retarded earlier in light-weight wood than in wood of greater specific gravity.

Although moisture content is one of the most important factors in the degradation process, ecological studies on this subject are few. Pechmann *et al.* (1967) carried out one of the most thorough investigations on the process of seasoning involving fungus attack and degradation of *Picea* logs stored for a period of 1 year with and without bark and at different localities with varying microclimates. Depending on the microclimate and logging time, the seasoning process in debarked wood was rather rapid but not uniform in all layers of the wood. Wood having a moisture content of between 60 and 100% of the dry weight in the outer layers was decomposed rapidly in these layers. Wood having a moisture content of below 30% and above 120% was not attacked. In most localities the 30% level was reached during the summer. An analogous situation might be expected in trunks with bark which have been heavily infested by insects. In logs with bark, the moisture content after 1 year was still high—between 100 and 200%—and no fungal attack was observed except in the cross-cut profiles where the dangerous half-moist condition was obtained.

Pechmann *et al.* (1967) found after 2 weeks no fungus attack on the logs; after 4–5 weeks Ascomycetes of the blue-stain group appeared and were followed by moulds. Next followed Basidiomycetes causing red stain, mainly *Stereum sanguinolentum* and *S. areolatum*. Fungi of the brown-rot type appeared sporadically during the first months but increased in number later. Numerous species were found to occur side by side in the logs. The antagonistic encounters between fungi of different groups were tested in laboratory. Wood initially colonized by blue-stain and mould fungi showed a less vigorous decay in the subsequent attack by *Stereum* species than sound wood which was attacked. Wood initially colonized by *Stereum* decayed much more rapidly during a subsequent brown-rot attack than healthy wood.

Henningsson (1967*c*) investigated the seasoning of unpeeled *Betula* and *Populu tremula* pulpwood during a storage period of 3 years. Both woods dried about equally during the first summer's storage. From the beginning of the second year, *Betula* wood dried very slowly whilst the *Populus* wood dried rapidly as a consequence of the general shedding of bark. Drying continued to the end of the third year; in birch wood from 85–91% moisture at the beginning to 51–67% at the end of the study and in aspen from 84–118% to 31–52% (Fig. 9). In laboratory tests both aspen and birch fungi were able to decompose wood with a moisture content within a range of 35–160%, though maximum decay was only obtained between 60 and

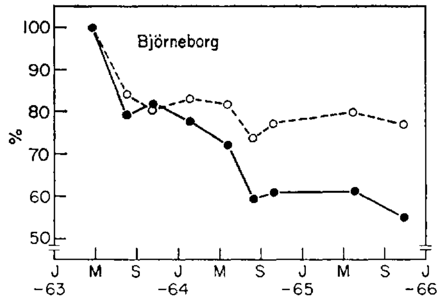

Fig. 9. Changes in the moisture content of undebarked *Betula* (—) and *Populus* (– – –) logs during storage. The moisture content given as per cent of the original moisture content of the wood. Björneborg, Central Sweden. (Reproduced with permission from Henningsson, 1967*c*, p. 20.)

120%. Thus, during 3 years the wood of the unpeeled logs of birch and aspen had a moisture content approaching the optimum for decay fungi. On birch, the sequence of fungi, observed both by sporophores and isolation, began with *Corticium* spp. during the first summer. During the second year *Stereum purpureum* and *Peniophora incarnata* dominated together with *Libertella betulina*. In the third year, the *Stereum hirsutum* and and *Polyporus zonatus* group was common. The early colonizers decomposed wood only slowly, whereas later fungi were active wood destroyers. Almost all the fungi were of the white-rot type.

The influence of the moisture content of the wood on fungal colonization was clearly seen in decorticated poles standing in soil (Käärik, 1971). These showed a very clear gradient in moisture content, varying in normal and dry soils in Sweden between 50 and 90% (extremes between 40 and 120%) on subterranean parts and between 20 and 30% (or up to 40–60%) on the aerial parts (Fig. 10). Three groups of fungi could be distinguished: (1) those attacking only the moist subterranean parts, such as *Fomes annosus*, *Polyporus borealis*, *Merulius himantioides*, *M. pinastri*, *Poria vaillantii* and *Odontia bicolor*; (2) those principally attacking aerial parts, such as *Peniophora gigantea*, *Polyporus amorphus*, *Peniophora pithya*, *Stereum abietinum*, *Fomes pinicola* and *Polyporus abietinus*; *and* (3) those found on both aerial and subterranean parts, viz. *Coniophora arida*, *Sistotrema brinkmanni*, *Corticium laeve*, *Trametes serialis* and *Hypholoma capnoides* (Table V).

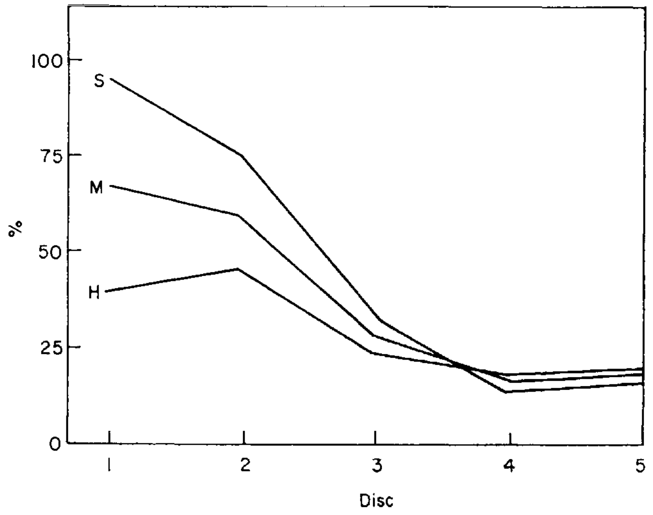

Fig. 10. Moisture content (% of dry weight) of *Picea* poles in dry sandy soil, Simlångsdalen, South Sweden, May 1971. Discs 1 and 2 in the soil; 3 at the soil surface; 4 and 5 above the soil.

No such clear distinction could normally be made as regards the blueing and soft-rot fungi: species of *Phialophora*, *Cladosporium*, *Ceratocystis*, *Verticicladiella* and *Rhinocladiella* were found on all parts of the poles. By contrast a very clear distinction appeared in species of Sphaeropsidales, such as *Discula pinicola*, *Sclerophoma pithyophila*, *Phomopsis* spp. and *Cytospora* spp., which were clearly concentrated in the aerial parts of the posts (Fig. 11). Fungi of Mangenot's stages 2–4 occurred on these posts until the last stages of decay and showed no clear succession.

Liese and Ammer (1964) studied the destruction of *Fagus* wood by soft-rot fungi in relation to the moisture content of wood. *Chaetomium globosum* and *Paecilomyces* sp. showed an increased capacity to attack the wood with increasing moisture content up to 240%. For *Ceratocystis*, however, an optimum was found at about 100%. *Trichoderma viride* appeared to be favoured by a high water content when aeration was sufficient. The lower limit for soft-rot activity was about 32–35%, which is somewhat higher than that for the decay fungi. The soft-rot fungi tested were able to survive dry periods as a consequence of an anabiotic phase during desiccation. The importance of the soft-rot fungi for the decomposition of the wood was found to be based, not so much on their deterioration capacity, as on their ability to grow under physiological conditions which prevent the growth of other funig.

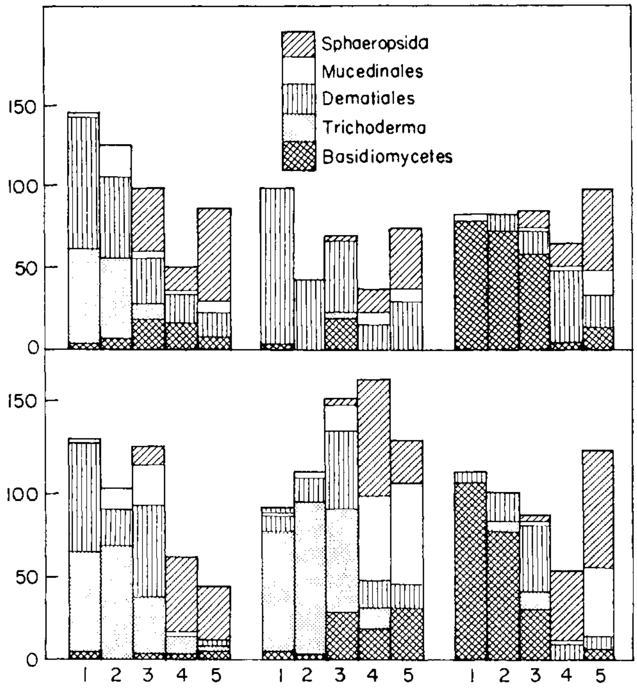

Fig. 11. Colonization of poles standing in soil by different groups of fungi. *Pinus*, after 6 months (left); 12 months (middle); 30 months (right). Top: normal forest soil, with weak colonization by *Trichoderma* in early stages. Below: dry, sandy soil, with strong colonization by *Trichoderma* in early stages. Discs 1 and 2 beneath the soil, 3 at the soil surface, 4 and 5 above the soil. Sphaeropsidales mainly above the soil. Numbers of isolations in 120 samples. (Käärik, 1971, p. 28.)

3. Carbon Dioxide

Carbon dioxide content and its influence on the growth of morphology of wood- and litter-inhabiting Basidiomycetes in Finland was investigated by Hintikka and Korhonen (1970). The highest concentration of CO_2 in wood was 11·4%, the average content was about 1·6% in conifer wood and 3·5% in deciduous trees. Accumulated carbon dioxide causes a rapid growth of vegetative mycelium within the wood, which, when it reaches normal air at the surface of the wood, begins to produce reproductive structures, while in some species growth itself is inhibited. Wood-inhabiting Basidiomycetes show a far greater tolerance to CO_2 than the litter-decomposing species.

4. pH

Tolerance of a comparatively wide range of pH, at least 4·0–9·0, and a growth optimum between pH 5·0 and 6·0, was found to be general among the wood-inhabiting fungi isolated and tested by Butcher (1966). Some, especially among the Basidiomycetes, had more specific requirements producing measurable growth only between pH 4·0 and 6·5. Tolerance of acidity was found to be greater in wood-inhabiting than in litter-decomposing Basidiomycetes (Hintikka, 1969). Henningsson (1967*a*) found that the pH optimum for mycelial growth for Basidiomycetes in *Betula* and *Populus* was between 5·0 and 6·0 with a wide tolerance between 1·5 and 8·0; the brown-rot fungi tolerated the lowest values and were more sensitive to high pH values.

Mangenot (1954) showed that pH fell to 4·4 when Basidiomycetes invaded tissues previously inhabited by blue-stain fungi. However, when Basidiomycetes invaded the wood first and were followed by the blueing fungi, the pH of the wood increased. These pH changes were assumed to be important factors affecting the competition of organisms in wood.

In synecological and autecological studies on the influence of pH on soft-rot microfungi, Sharp and Eggins (1970*b*) found the optimal pH for isolation and cellulolytic activity to be between 6·0 and 7·0. Some species were indifferent to changes of the pH whilst others were very sensitive. The pH of the wood had a definite influence in determining the dominant species of fungi and losses of wood strength.

5. Nitrogen Content

Among the nutritional factors, nitrogen content of the wood has been found to play the most important role. Mature woody tissues contain very little nitrogen, about 0·03–0·10%, as compared to 1–5% by weight for most herbaceous tissues. The C:N ratio of most wood species is between

350:1 and 500:1, in some species even 1250:1, as in *Picea sitchensis* (Sitka spruce) (Cowling, 1970). Wood-destroying fungi are able to utilize large amounts of carbohydrates and lignin in the presence of relatively small amounts of nitrogen. These fungi apparently have a very efficient mechanism for its metabolism and conservation. The role of nitrogen in wood decay has been reviewed by Cowling (1970). As a result of the attack of different wood-decay fungi, the weight loss was found to show a highly significant and direct correlation to the nitrogen content of the individual annual increments. Results of experiments *in vitro* supported the theory that in wood-decay fungi the autolysis and re-use of nitrogen in their own mycelium, or the lysis of other fungi present in wood during decay and an extremely economical use of nitrogen in metabolism, could contribute to the ability of wood-destroying Basidiomycetes to conserve the small amount of nitrogen in wood (Levi *et al.*, 1968).

6. *Geographical Situation and Altitude*

The attack of decay fungi at different altitudes in the Alps was investigated by Wälchli (1970*a*, *b*). The height above sea level alone was not an important factor. In the subalpine zone, toward the upper limit of tree growth, about 1000–1700 m, numerous common decay fungi for coniferous wood were found, with *Lenzites abietina* and *L. sepiaria* the dominant species. In the alpine zone, 33 Basidiomycetes, 3 Ascomycetes and 2 Myxomycetes were also found to attack the avalanche barriers. Here too, *Lenzites abietina* and *L. sepiaria* dominated in wood exposed to the air and *Poria versipora*, together with other *Poria* species and Thelephoraceae common in the colline and montane zones, attacked near the ground. The alpine zone is not in itself free from wood-destroying fungi but the attack depended on the presence of wood. Many of the active decay fungi and lignicolous micromycetes are cosmopolitan.

A formula based on U.S. Weather Bureau summaries was developed by Scheffer (1971) to yield an index of the relative potential of a climate to promote decay in off-the-ground wood structures. After adaption, the formula was also deemed to meet conditions of wood in contact with the ground.

D. Interrelations Between Micro-organisms

It is a well established fact that micro-organisms growing together on a substrate interact in various ways. Much of the laboratory work has been done on this subject on artificial media. These studies have shown that the mutual action between two organisms is entirely dependent on external factors such as nutrition, temperature and substrate acidity (Oppermann, 1951; Vaartaja and Salisbury, 1965; Henningson, 1967*b*; Keyes, 1966). Changes in these factors can easily result in conversion of mutual effects, and the results on artificial media must therefore be regarded with great caution in the discussion of interactions in natural substrates. In relations between fungi or fungi and bacteria, antagonistic effects seem to be more common than synergistic associations.

Kerner-Gang (1970) studied the interrelationship of fungi occupying stakes. The wood-inhabiting fungi, especially *Penicillium* spp. developed first and inhibited or suppressed the wood-destroying fungi. In series without *Penicillium*, *Trichoderma* or *Gliocladium* appeared first and inhibited other fungi, especially the *Phialophora* species. In long-term tests Käärik (1971) obtained differing results on wooden posts in soil, where a very heavy infection of *Trichoderma* was found on certain soils in the early stages of degradation. During the following years posts on the same plots were attacked by decay fungi to the same or a greater extent than on plots with a weak attack of *Trichoderma* (Fig. 11). If some retarding effect was caused by this fungus on the decay, it was not distinguishable from the effect of other micro-organisms on other plots. Attack by *Penicillium* during a period of 4 years was extremely rare in wood more than 3–5 mm below the surface.

The interaction of soft-rot fungi on *Fagus* wood has been studied by Liese and Eckstein (1967). During successive and simultaneous attacks on saturated wood, the soft-rot fungi tested showed no mutual effects but in air-dried wood the weight losses were usually reduced as compared with single species attack. Sharp and Eggins (1970*a*) examined the hyphal mixing and deterioration of *Fagus* wood by pairs of soft-rot fungi. Some reduced cellulolytic activities and in others more stimulated reactions were observed. No distinct antagonism occurred whereby the decay activity of a species was completely prevented and similarly no single fungus enhanced or inhibited all the fungi it encountered. Examples of partial inhibition and enhancement of one fungus by another were found, but since there was no pattern to these results they were interpreted as manifestations of incubation conditions. Bourchier (1961) studied the effect of microfungi on Basidiomycete decay in wood of *Pinus* and found both inhibitory and synergistic effects. Stillwell (1966) found that in the presence of *Cryptosporiopsis* sp., decay was reduced in both *Betula* wood and logs of *Abies balsamea*. Both inhibiting and stimulating effects on decay by basidiomycetous fungi on *Betula* and *Populus* sapwood were also found by Henningsson (1967*b*) with different strains of bacteria. Fungistatic effects of ground up thallus and extractives of some epixylic lichens on various decay fungi were shown by Rypáček (1966) and Henningsson and Lundström (1970).

E. Rate of Degradation and Conclusions

In one-species decay tests under laboratory conditions, the degradation of wood by decay fungi may be very rapid and, within certain limits, species characteristic. During a period of 12–16 weeks the most active fungi caused losses of dry weight of about 60–70% (Table IV), giving a microscopic picture of attack comparable to those in the late stages of decay in nature, but on natural sites decomposition is not usually so rapid. At favourable sites in the northern humid climate zone de-barked posts standing in soil may reach an advanced stage of decay after 4 years; de-barked medium-sized logs and branches lying on the ground or stored under humid conditions may also reach a stage of advanced decay after the same period. Coniferous stumps in South Sweden were strongly decayed after 5–6 years under humid conditions, but in North Sweden they could last for more than 20 years. In East Anglia 20–30-year-old coniferous stumps were destroyed after 8–9 years (Meredith, 1960). In standing dead trees, wood is rapidly seasoned and the degradation processes almost cease after the bark is peeled off, so that such trees have been reported to be standing 20–40 years or longer after their death. Degradation is also very slow in branches dying in the crowns of the trees: in larger branches successions lasting 20 years and longer have been reported. Even if the variable temperature and moisture relations are taken into account the degradation process in nature is considerably slower than the one-species attacks in the laboratory, which means that the most aggressive fungi do not dominate during the whole decay process and that the action of different micro-organisms simultaneously and in succession retards the degradation process.

In the primary colonization and during the following succession of fungi, the moisture content of the wood is a decisive factor. Successions in wood with a similar and rather rapid seasoning process, as in standing insect-killed or fire-killed and wind-thrown trees, show a rather similar pattern beginning with blue-stain fungi, followed by moulds and decay fungi, often with the same species dominating on different kinds of trees. Other successions were found in wounded standing trees with a high moisture content, with bacteria and rather few non-decay fungi as pioneer species, followed by decay fungi, or beginning directly with aggressive saprophytes. After the death of the trees, under humid conditions numerous species and variable successions may continue the decomposition. In felled trunks and logs with the bark still intact, attack is also dependent on the seasoning process. Numerous non-decay fungi and less active decay fungi are among the pioneer invaders and the active decay fungi appear later, attacking already occupied wood. As compared with the above successions, the fungus flora on de-barked wooden posts standing in soil is especially rich in species. Most of the non-decay fungi may be found from the first to the last stages of decay but the different species culminate at different times. The most active decay fungi again first appear at the later stages of decay, and the sequences in decay do not resemble those on stumps and standing trees.

These successions cannot be brought within a general schema. Difficulties arise even as compared with Garrett's very broad stages (p. 148). It is difficult to distinguish between primary and secondary moulds and in most wood substrates the white-rot fungi are already dominant among the earliest colonizers in dead wood.

The successions analysed generally show that in wood degradation not only are decay Basidiomycetes of importance but that bacteria and non-decay fungi are involved from the beginning of the decomposition process in living trees. The degradation of wood is a long and complicated procedure, depending on the complexity of the wood material itself, the physical and chemical factors influencing this substrate and the interactions between micro-organisms and wood and the micro-organisms themselves.

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